

A morphometric exploration of the taxonomic utility of scale osteoderms in southern African fossorial skinks (Acontinae, *Acontias*)

Zhongning Zhao¹, Lucas Thibedi^{2†}, Mphalile Mokone², Neil Heideman²

¹ Department of Genetics, Faculty of Natural and Agricultural Sciences, University of the Free State, P.O. Box 339, Bloemfontein, 9300, South Africa

² Department of Zoology and Entomology, Faculty of Natural and Agricultural Sciences, University of the Free State, P.O. Box 339, Bloemfontein, 9300, South Africa

<https://zoobank.org/997B9DA2-9F64-492C-82A5-A86D80749313>

Corresponding author: Zhongning Zhao (orochi19851020@yahoo.com)

Academic editor: Johannes Penner ♦ Received 5 October 2024 ♦ Accepted 26 March 2025 ♦ Published 1 July 2025

Abstract

This study investigates the morphometric variation of osteoderms across species and populations within the genus *Acontias*, especially in the *A. meleagris* species complex. Using both univariate and multivariate analyses, we evaluated whether size-independent osteoderm morphometrics could effectively differentiate taxa, particularly where minimal genetic divergence is present (i.e., cases where morphologically diagnosable species show little genetic separation). Univariate analysis revealed some significant morphometric variation across osteoderm regions, with sub-regions C and D showing the highest discriminatory power. Multivariate analyses, including principal component analysis (PCA) and discriminant function analysis (DFA), demonstrated the complementary strengths of ratio-based and studentized linearized residuals (SLRs)-based metrics. Ratio-based analyses were more effective in distinguishing genetic species, while SLRs-based analyses captured finer-scale population differences. The combined approach improved classification accuracy, underscoring the value of integrating multiple morphometric methods. Our results suggest that osteoderm morphometrics provide valuable supplementary data for species delimitation and may help resolve taxonomic boundaries within *Acontias* and possibly other lizards. However, the limited ability to differentiate morphs and populations in some cases highlights the need for additional data, such as environmental or behavioral traits. The findings have the potential to improve taxonomic resolution among skinks and contribute to broader taxonomic frameworks in herpetological systematics.

Key Words

Legless lizard, morphology, multivariate analysis, size-independent, skink, species delimitation, studentized linearized residuals, ratios, reptile

Introduction

Osteoderms are plates comprising mainly calcium phosphate and collagen found in the epidermal scales of many tetrapods, including crocodilians, squamates, certain frogs, armadillos, and some extinct taxa (Boulenger 1887; Camp 1923; Oliver 1951; Strahm and Schwartz 1977; Hill 2005; Williams et al. 2022). These structures exhibit significant variation in number, shape, and sculpturing and may

therefore potentially be of use as diagnostic characters in taxonomic studies. Closer examination of their utility has, however, led to varying views. For instance, Boulenger (1887) argued that osteoderms were too variable at the intraspecific level to be taxonomically informative, while others, including Camp (1923), Hewitt (1929), Hoffstetter (1962), and Lambiris (1992), considered them valuable taxonomic markers. Camp (1923) notably emphasized the importance of comparing osteoderms from identical

† Deceased.

body regions to ensure diagnostic accuracy. Strahm and Schwartz (1977) found them to be diagnostic up to genus level in the Diploglossinae and Anguidae, while Burns (2008) demonstrated their taxonomic relevance in ankylosaurid and notosaurid ornithischian fossil taxa. Osteoderms have been attributed various functions beyond their taxonomic significance, including defense against predators and protection during intraspecific combat (Vickaryous et al. 2015). Furthermore, Broeckhoven et al. (2015) experimentally demonstrated that osteoderms provide protection by reducing skin penetration from simulated bites of different mongoose species, supporting their role in predator defense. Additional proposed roles include thermoregulation, nutrient storage, and water retention (Williams et al. 2022). The thermoregulatory function of osteoderms has been linked to their vascularization, although this remains debated, with most studies focusing on crocodilians and turtles rather than squamates (Williams et al. 2022).

In lizards, comparative lepidosis remains the primary method for taxonomic diagnosis and is expected to continue being an indispensable component of taxonomic keys due to its practicality and wide application. Prominent taxonomic references for skinks, such as those by FitzSimons (1943), Broadley and Greer (1969), and Branch (1998), are all primarily based on lepidosis. However, the diagnostic potential of osteoderm polymorphism, particularly in skinks, remains underexplored. Skink osteoderms are relatively simple in structure and morphology (see fig. 3 in Williams et al. (2022) for detailed descriptions of Scincidae), making them easier to quantify and analyze compared to the more complex osteoderms found in anguid lizards. For detailed structural descriptions of Anguidae, see figs 1, 2 in Strahm and Schwartz (1977). This simplicity offers an advantage for morphometric comparisons, facilitating the testing of osteoderms as a reliable diagnostic feature among skinks. Such testing could yield significant insights, not only within skinks but also across other lizard taxa that exhibit similarly straightforward osteoderm structure. The taxonomic importance of osteoderms lies in their potential to enhance phylogenetic analyses by integrating multiple diagnostic traits. Recent findings by Daza et al. (2024) have demonstrated that osteoderms are not only morphologically informative but also provide evolutionary insights. These findings highlight the role of osteoderms in elucidating phylogenetic relationships among both extant and extinct skink species. As a result, osteoderms could serve as a crucial trait in systematics, complementing other morphological and molecular data, and thereby strengthening the resolution of phylogenetic hypotheses across lizard taxa.

The taxonomy and species boundaries within the morphologically conservative legless skink subfamily *Acontinae* have long been considered ambiguous and challenging to delineate (Zhao et al. 2023). Molecular evidence has recently shed light on these complexities, revealing that *Acontias occidentalis* is closely related to *Acontias percivali*, with the latter being nested within the *A. occidentalis* species complex (Zhao et al. 2023). Furthermore, despite *Acontias lineicauda* showing a close phylogenetic relationship to the *Acontias meleagris* species complex (Daniels et

al. 2005, 2009; Engelbrecht et al. 2013), the genetic distance between *A. lineicauda* and other members of the *A. meleagris* complex remains significant (Zhao et al. 2023). Further molecular analyses have resulted in the synonymization of previously recognized species, such as *Acontias percivali tasmani* and *Acontias orientalis*, with *A. meleagris* (Daniels et al. 2005, 2009; Engelbrecht et al. 2013; Zhao et al. 2023). Moreover, considerable genetic divergence has been detected among lineages within the *A. meleagris* complex. For instance, individuals from the Coega area, which were identified morphologically as “*A. p. tasmani*”, and geographically distant populations from Mossel Bay were found to belong to the same clade. In contrast, populations of *A. meleagris* from Robben Island and Saldanha Bay form a distinct, separate clade (Daniels et al. 2005, 2009; Engelbrecht et al. 2013). These findings emphasize the intricate evolutionary history and taxonomic complexity within the *Acontinae*, underscoring the need for integrative approaches combining molecular and morphological data.

In morphometric taxonomy, both studentized linearized residuals (SLRs) and ratios are integral to multivariate analyses such as principal component analysis (PCA) and discriminant function analysis (DFA) (Rohlf 1990; Zhao et al. 2021). Each approach offers distinct advantages and limitations, making them appropriate for different research contexts. Ratios are especially useful for capturing relative differences between measurements, which is crucial for differentiating species or populations based on body proportions. They are widely employed in morphometric studies, particularly in taxonomy, where body size comparisons are pivotal (Baur and Leuenberger 2011). Ratios facilitate the scaling of body size effects and can be interpreted within the framework of allometry, which pertains to shape changes related to size. However, a significant drawback of ratios is their sensitivity to size differences, which can sometimes obscure true shape variation by conflating size-related and shape-related differences. Additionally, when ratios are directly applied in multivariate methods like PCA, they may not fully capture complex shape relationships unless appropriately adjusted for size (Courtenay 2023). SLRs, on the other hand, are derived by adjusting the residuals from regression analyses for variability, making them a robust tool for size correction. They are particularly valuable in controlling for body size effects, providing a clearer representation of shape variation independent of size. SLRs are advantageous when the focus is on shape differences without the confounding influence of size (Baur and Leuenberger 2011; Lehmann 2012). Nonetheless, SLRs also present challenges, including their computational and interpretative complexity compared to ratios, which requires a more profound statistical understanding. Moreover, in datasets with high variability, even well-standardized residuals may not entirely negate the influence of size (Baur and Leuenberger 2011; Courtenay 2023).

In this study, we aimed to evaluate the taxonomic utility of osteoderms in distinguishing among several fossorial skink species: *Acontias occidentalis*, *A. percivali*, *A. lineicauda*, *A. meleagris*, and the morphs “*A. orientalis*” and

“*A. p. tasmani*” (Lamb et al. 2010). The distribution of these species is as follows: *A. meleagris* is found along the southern coast of South Africa; *A. occidentalis* occurs in parts of Angola, Namibia, Botswana, Zimbabwe, and South Africa; *A. percivali* is restricted to southeastern Kenya; *A. lineicauda* is native to the area around Port Elizabeth and Port Alfred in the Eastern Cape Province of South Africa; and the “*A. p. tasmani*” and “*A. orientalis*” morphs are found in the Eastern Cape Province (Broadley and Greer 1969). We hypothesized that (i) distinct species could be reliably differentiated based on osteoderm morphometrics from corresponding body regions, with closely related morphospecies exhibiting smaller morphometric distances compared to more distantly related ones; (ii) osteoderm characteristics would be invariant (fixed) within populations of the *A. meleagris* species complex; and (iii) both ratios and SLRs would provide informative morphometric data in multivariate analyses to differentiate among taxa.

Materials and methods

Specimens from the following localities were analyzed, with a consistent sample size of ten per group:

Acontias occidentalis (Windhoek, Namibia [22.5609°S, 17.0658°E]), *Acontias percivali* (Voi, Kenya [3.3961°S, 38.5633°E]), and “*Acontias p. tasmani*” (Coega, Eastern Cape Province, South Africa [33.8020°S, 25.6883°E]). Additionally, *Acontias lineicauda* (Port Elizabeth, Eastern Cape Province, South Africa [33.7174°S, 25.8142°E]) and “*Acontias orientalis*” (Port Elizabeth, Eastern Cape Province, South Africa [33.7521°S, 25.6995°E]) were included (Fig. 1). Furthermore, samples were obtained from three geographically distinct populations of *Acontias meleagris* in the Western Cape Province (Fig. 1), with the following sample sizes: Mossel Bay ([34.1831°S, 22.1460°E], $n = 10$), Robben Island ([33.8066°S, 18.3662°E], $n = 5$), and Saldanha Bay ([33.0117°S, 17.9443°E], $n = 8$). A GIS map was generated using QGIS Geographic Information System (QGIS Development Team, 2023), version 3.30.2, employing the Natural Earth II 10 m raster dataset (available at: <https://www.naturalearthdata.com/downloads/10m-raster-data/10m-natural-earth-2/>). All spatial data were projected using the WGS 1984 coordinate reference system. All specimens had a snout-vent length greater than 80% of the maximum published for the species (Branch 1998) and were therefore considered adults.

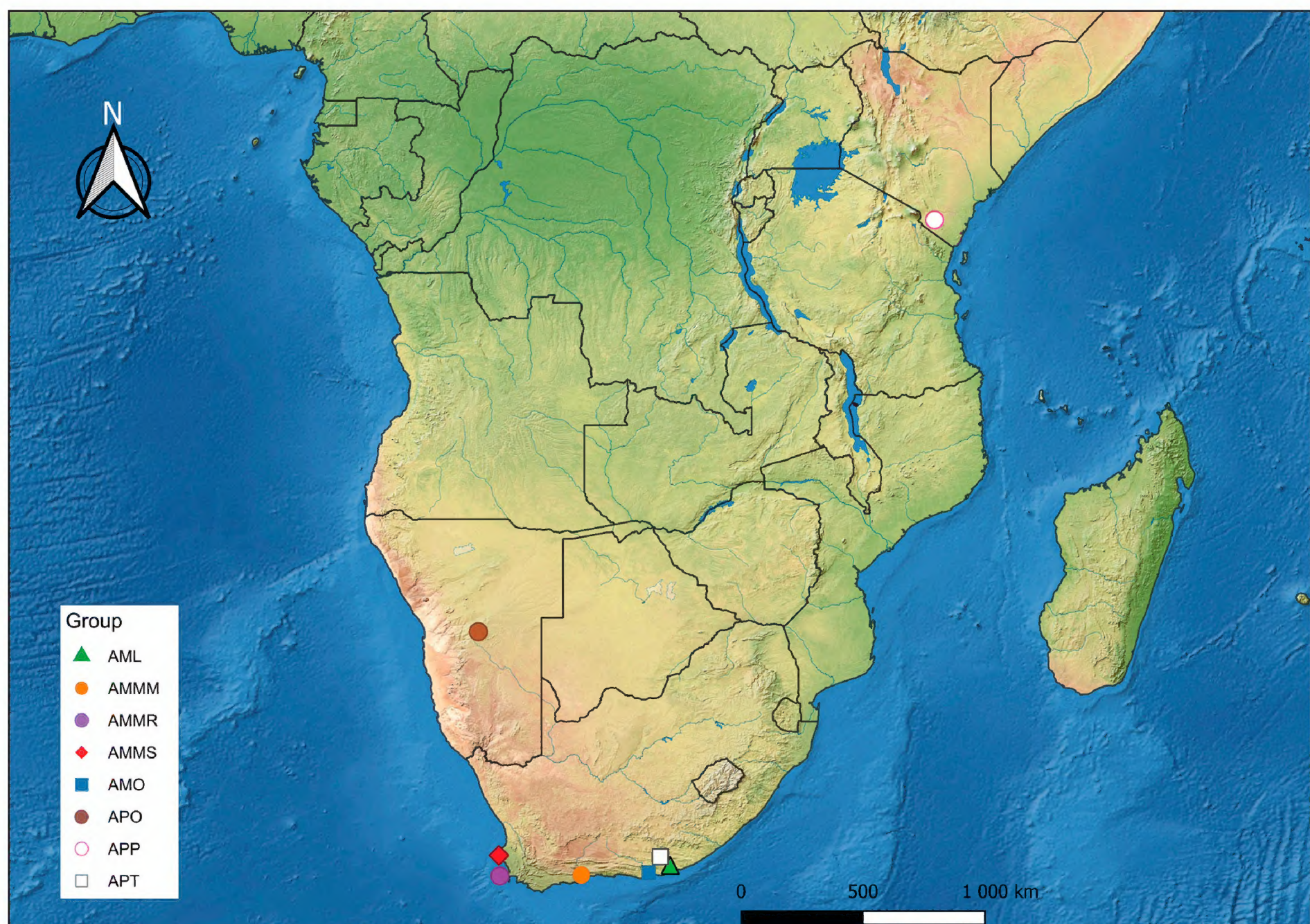


Figure 1. Map illustrating the sampling locations for this study. Abbreviations: “AMO” = *Acontias orientalis*, “AMMM” = *Acontias meleagris* (Mossel Bay population), “AML” = *Acontias lineicauda*, “AMMS” = *A. meleagris* (Saldanha Bay population), “AMMR” = *A. meleagris* (Robben Island population), “APO” = *Acontias occidentalis*, “APP” = *Acontias percivali*, and “APT” = *Acontias percivali tasmani*. The map was generated using QGIS v3.30.2 (QGIS Development Team) with the Natural Earth II 10 m raster dataset (available at Natural Earth: <https://www.naturalearthdata.com/downloads/10m-raster-data/10m-natural-earth-2/>). Blue lines represent rivers, while black lines indicate country borders.

Scales were collected from five body regions: the mid-dorsal body (MDB), mid-ventral body (MVB), the pre-anal scale (PA), mid-dorsal tail (MDT), and mid-ventral tail (MVT). The complete set of osteoderms was extracted from each specimen. For species with a sample size of 10, this meant that one MDB osteoderm was removed from each individual, resulting in a total of 10 MDB osteoderms. The same approach was applied to all osteoderm types, ensuring a consistent sample size of 10 for each category. The preparation of scales followed the method developed by Lambiris (1992). This process involves first severing Sharpey's fibers, which anchor the osteoderm between adjacent ones, by carefully sliding a fine-pointed blade across its anterior dorsal and anterior ventral sides. The osteoderm is then grasped posteriorly with fine forceps and gently pulled in a caudal direction for removal. Extracted osteoderms were stored individually in tubes containing alcohol. Scales were cleaned by macerating in 5% KOH and carefully removing connective tissue with fine forceps. They were then stained with a solution of 0.5M Alizarin Red in 5% KOH until the osteoderms were sufficiently highlighted. After staining, scales were dehydrated through sequential immersions in 70%, 96%, and 100% ethanol (EtOH), each for three minutes, followed by five minutes in xylene. The scales were mounted on microscope slides but were not cover-slipped. A diagram illustrating the basic structure of an acontine scale's osteoderms is presented in Fig. 2. The osteoderms of each scale were

subdivided into four sub-regions (sub-regions A–D) as shown in Fig. 3. In the case of the PA scale, this was, however, not possible as its osteoderms could not be readily grouped. Size and area determinations were made by scanning the scales to a computer and analyzing them using the Soft Imaging System analySIS Program (Soft Imaging System GmbH Master). For the PA scale, only the total area was recorded (for the measurement data, see Suppl. material 1).

We normalized the dataset using a log transformation in R version 4.2.2 (R Core Team 2022). To assess and confirm the normality of the dataset, we applied the Kolmogorov-Smirnov test using the R package 'nortest' (Gross and Ligges 2015), and all log-transformed variables yielded a p-value greater than 0.05 (no significant deviations from the normal distribution), indicating significant improvement in data normality. For the statistical analyses, we first identified informative variables for distinguishing among groups through one-way analysis of variance (ANOVA) as a univariate approach, using the R packages 'car' (Fox 2023) and 'DescTools' (Signorell et al. 2019) in R version 4.2.2. To adjust for multiple comparisons, we applied the Bonferroni correction post-hoc test, which rebalances the compounding risk of Type I error by adjusting p-values. Two independent ANOVA analyses were conducted: (1) ANOVA based on the log-transformation of each variable (without accounting for body size variation), and (2) ANOVA based on ratios, where each

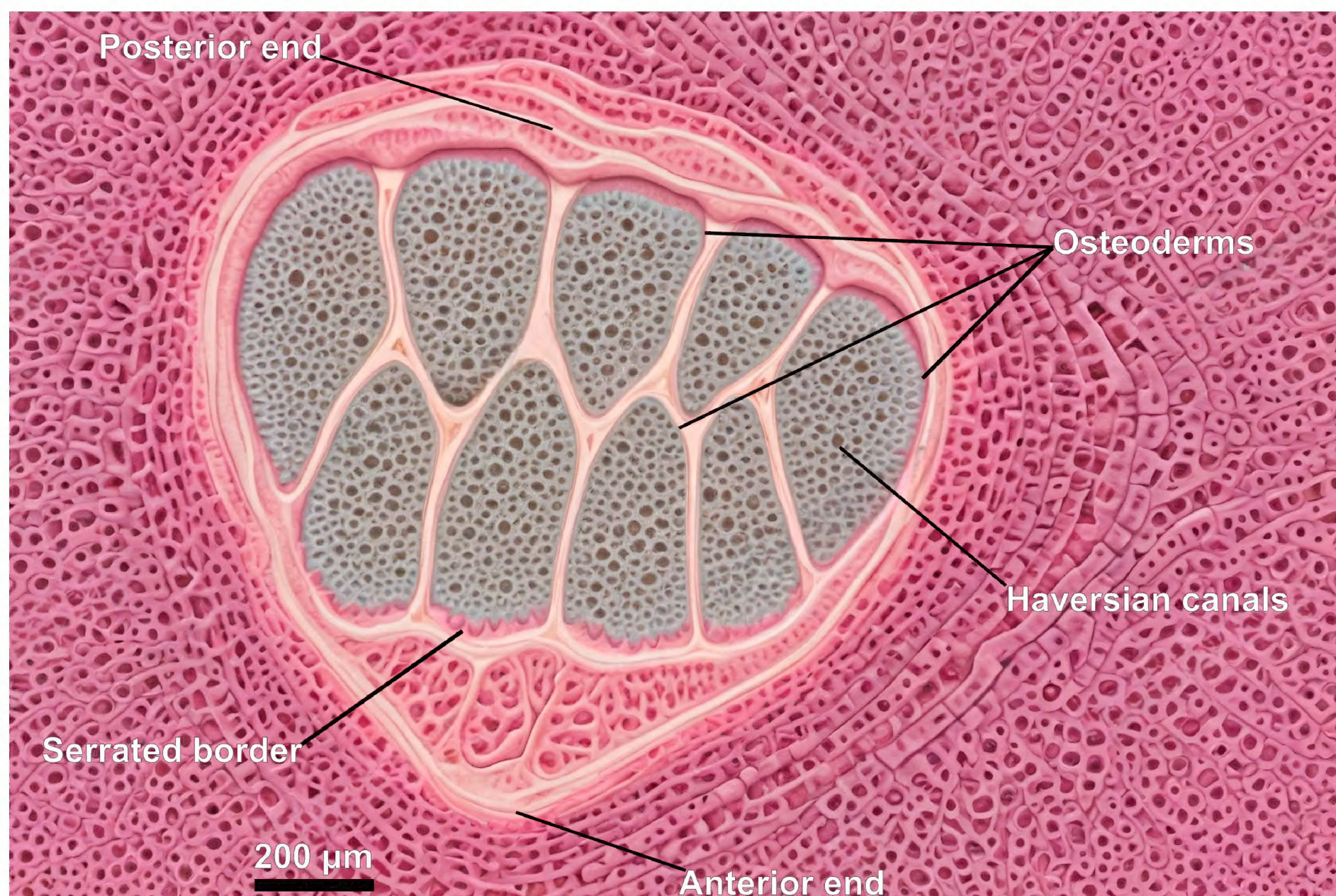


Figure 2. Illustration of the osteoderm anatomical structure of the acontine skink (represented by *Acontias orientalis*), with scale units indicated.

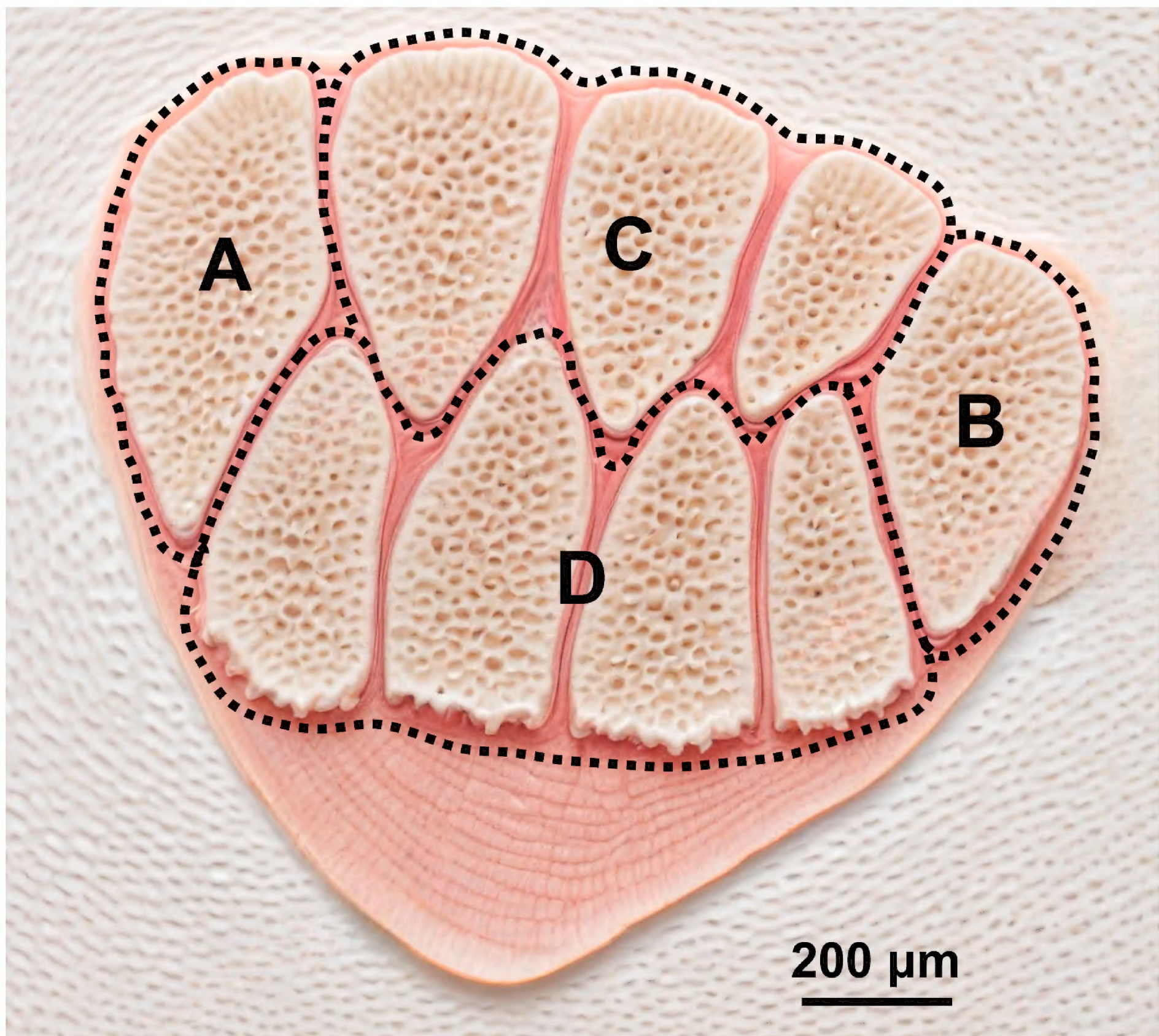


Figure 3. Illustration of the four sub-regions (A–D) into which each osteoderm (represented by *Acontias orientalis*) was divided, with scale units indicated.

variable representing areas of different sub-regions of the four anatomical regions (MDB, MVB, MDT, and MVT) was divided by the area of the PA (to account for proportional size and the effect of body size variability). We also performed analysis of covariance (ANCOVA) to assess the effect of body size using PA as the covariate, applying the R packages ‘emmeans’ (Lenth 2023) and ‘car’ (Fox 2023). The Bonferroni correction was again applied for post-hoc pairwise comparisons to evaluate significant differences between groups.

To test the first and second hypotheses, we employed multivariate analyses—PCA and DFA—to evaluate whether osteoderm area morphometrics could effectively differentiate between groups. First, PCA was used to reduce dimensionality through the R packages ‘factoextra’ (Kassambara 2016) and ‘factoMineR’ (Lê et al. 2008), allowing us to explore whether the reduced dimensions could reveal any diagnostic separation of taxa or populations without bias from pre-

defined groupings (Courtenay 2023). We then used DFA, which incorporates grouping bias (Baur and Leuenberger 2011; Courtenay 2023), to assess whether each taxon or population could be correctly classified based on osteoderm morphometric data, utilizing the R packages ‘caret’ (Kuhn 2015) and ‘mass’ (Venables and Ripley 2002). To test the third hypothesis, we conducted PCA and DFA independently on (1) studentized linearized residuals (SLRs) of all variables (after transformation in R version 4.2.2) and (2) ratios of all variables divided by PA. Both approaches were employed to account for body size effects and to either remove or reduce these effects (Baur and Leuenberger 2011; Courtenay 2023). Lastly, we performed a combined PCA and DFA analysis using an integrative dataset that included both ratios and SLRs. During the DFA analysis, we applied the “remove-collinear-vars” function to eliminate highly collinear variables, using a threshold of 0.95 as the selection criterion.

Results

Univariate analysis

For the univariate analyses, both the log-transformed variable-based ANOVA (Suppl. material 2) and the ANCOVA (Suppl. material 3) consistently revealed significant morphometric differences across taxa and groups in all osteoderm regions and sub-regions ($p < 0.05$). Additionally, the ratio-based ANOVA (Suppl. material 4) demonstrated significant area-based morphometric differences across taxa and groups in most variables ($p < 0.05$), with the exception of the B sub-region in the MDB and MVB regions ($p > 0.05$). Collectively, the univariate analyses underscore the presence of significant osteoderm morphometric variation across certain taxa and populations, independent of body size effects.

Post-hoc analyses (post-hoc results not shown) further indicated that all four anatomical regions (MDB, MVB, MDT, and MVT) contained substantial morphometric information capable of distinguishing between different species, particularly genetically distinct taxa such as *A. lineicauda*, *A. percivali*, *A. occidentalis*, and the *A. meleagris* species complex (*A. p. tasmani*, *A. orientalis*, and the three populations of *A. meleagris*). However, these variables were less effective in differentiating the three *A. meleagris* populations and *A. orientalis* within the *A. meleagris* group. Interestingly, despite molecular phylogenetic studies suggesting *A. p. tasmani* is synonymous with *A. meleagris* (Daniels et al. 2005, 2009; Engelbrecht et al. 2013; Zhao et al. 2023), many osteoderm characters, especially in sub-regions C and D, revealed substantial morphometric differences between *A. p. tasmani* and the other groups within the *A. meleagris* complex ($p < 0.05$). Furthermore, post-hoc tests consistently showed morphometric differences between *A. p. tasmani* and both *A. percivali* and *A. occidentalis* ($p < 0.05$), while the difference between *A. occidentalis* and *A. percivali* was not significant ($p > 0.05$).

Our findings align with genetic divergence patterns but generally failed to distinguish between morphs and populations within the *A. meleagris* group, with the exception of the distinct “*A. p. tasmani*” morph. Notably, post-hoc tests revealed a clear trend: sub-regions C and D retain more morphometric variation, offering greater discriminatory power between taxa and populations than sub-regions A and B. Of these, sub-region C emerged as the most robust delimiter for distinguishing between groups. This trend was particularly pronounced after accounting for body size effects using ratio-based ANOVA and log-transformed ANOVA with PA as a covariate. This would highlight the importance of taking into consideration the body size effect. No significant osteoderm morphometric differences were diagnosed between the four anatomical regions (MDB, MVB, MDT, and MVT), suggesting that all regions are similarly informative for distinguishing between taxa and certain populations.

Multivariate analyses

When visually assessing the PCA scatterplot (Fig. 4), the ratio-based PCA showed superior separation between different taxa, especially among genetically distinct species. In contrast, the SLRs-based analysis performed better at differentiating between morphs and populations within the *A. meleagris* complex but struggled to demarcate genetic species boundaries. Our principal component analysis (PCA) showed that the first two principal components (PCs) from the studentized linearized residuals (SLRs)-based analysis explained a substantial portion of the total variance (PC1: 64.30%, PC2: 9.29%). In contrast, the ratio-based analysis (PC1: 31.91%, PC2: 19.30%) and the combined approach (PC1: 33.89%, PC2: 17.27%) retained less variance (see Suppl. materials 5, 6: fig. S1) from the first two PCs. The integrated PCA approach, which combines both ratio and SLRs data, leveraged the strengths of each method, yielding improved separation between genetic species and distinguishing populations and morphs within the *A. meleagris* group. This suggests that a combined analysis adds substantial value over using either method in isolation. Moreover, across all PCA analyses, sub-regions C and D consistently contributed more to the overall variance than sub-regions A and B (Suppl. material 6: figs S2–S4), highlighting their importance in distinguishing morphometric variation. However, no significant bias was observed in the contribution of variance across the four broader anatomical osteoderm regions, indicating that all regions are equally informative in the context of our analyses.

Our DFA scatterplot (Fig. 5) closely aligns with the patterns observed in our PCA analysis. It reveals that the ratio-based DFA achieves better separation between genetic species, though it struggles to distinguish between morphs and populations within the *A. meleagris* complex. Conversely, the SLRs-based DFA excels at differentiating populations and morphs within the *A. meleagris* group but performs poorly when discriminating genetic species. The integrative approach, which combines both methods, successfully incorporates the strengths of each, substantially improving demarcation at both the genetic species level and within *A. meleagris* populations and morphs. In both the ratio-based (DF1: 75.48%, DF2: 7.84%) and SLRs-based (DF1: 48.74%, DF2: 35.42%) DFA analyses, the first two discriminant functions (DF) retained a significant portion of the total variance (Suppl. material 7). The Mahalanobis pairwise distance tests (Suppl. materials 8, 9) mirrored this trend, indicating that significant osteoderm morphometric differences were primarily observed between genetic species in the ratio-based analysis, but not among populations and morphs within the *A. meleagris* complex. In contrast, the SLRs-based analysis revealed some diagnosable distinctions between populations and morphs. The combined integrative analysis notably improved the discriminatory power, successfully capturing the advantages of both individual approaches. The DFA classification matrix supports this trend (see Table 1):

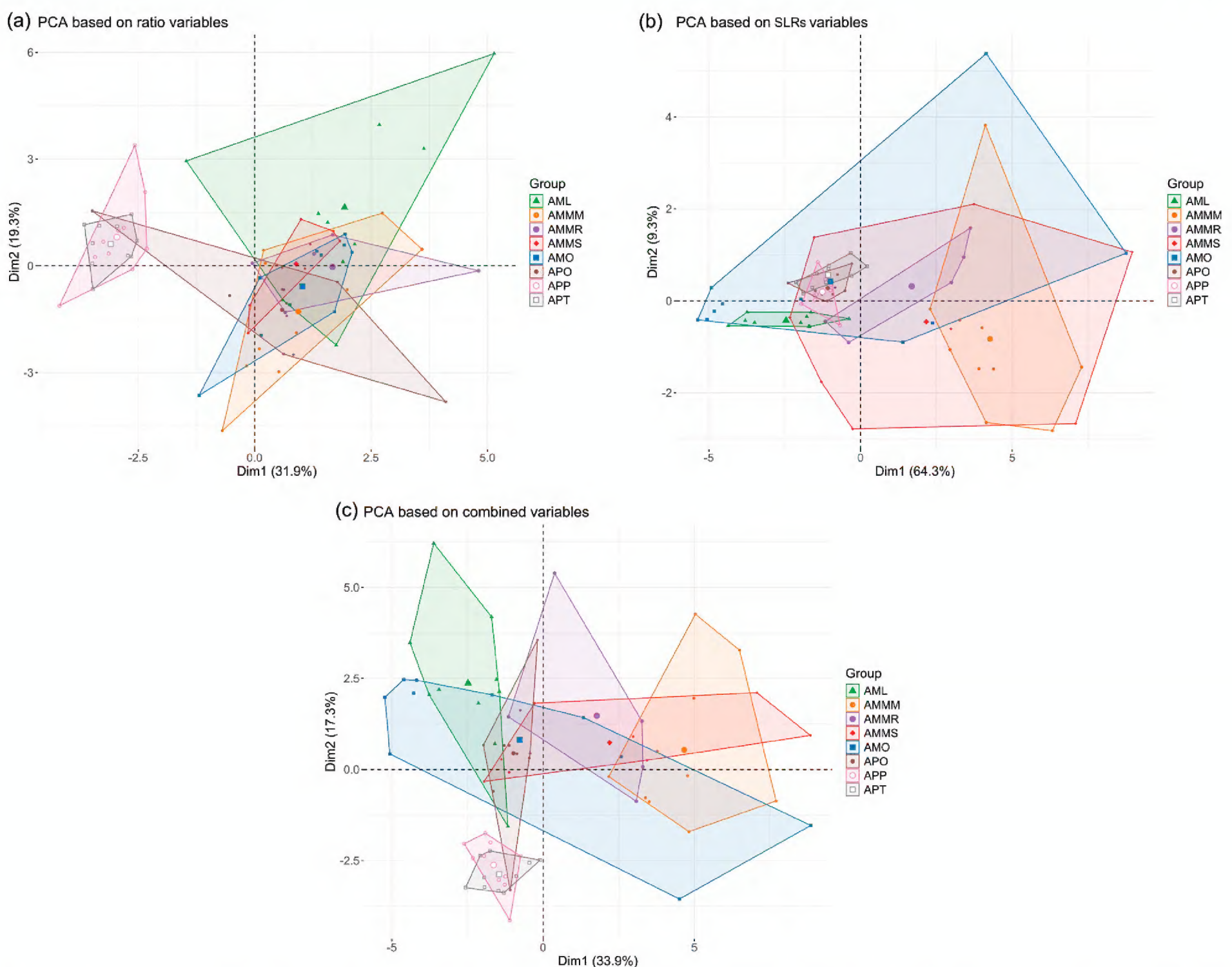


Figure 4. Principal component analysis (PCA) scatterplot of the first two principal components, which capture the highest levels of total variance. The analysis was performed independently using ratios, studentized linearized residuals (SLRs), and a combined approach. Abbreviations: “AMO” = *Acontias orientalis*, “AMMM” = *Acontias meleagris* (Mossel Bay population), “AML” = *Acontias lineicauda*, “AMMS” = *A. meleagris* (Saldanha Bay population), “AMMR” = *A. meleagris* (Robben Island population), “APO” = *Acontias occidentalis*, “APP” = *Acontias percivali*, and “APT” = *Acontias percivali tasmani*.

the ratio-based DFA demonstrated higher accuracy in predicting group membership at the genetic species level, while the SLRs-based DFA was more effective at identifying populations and morphs within the *A. meleagris* complex. However, the integrative approach led to significant improvements in prediction accuracy across all groups, reflecting a substantial enhancement in the overall analysis.

Discussion

This study examined the morphometric variation of osteoderms across four subregions of four body regions in selected species and populations of the genus *Acontias*, with a focus on distinguishing genetic species and populations within the *A. meleagris* species complex. Our primary objective was to determine whether osteoderm morphometrics could effectively differentiate between taxa and populations, consistent with genetic divergence patterns. We hypothesized that size-independent osteoderm metrics would offer sig-

nificant discriminatory power among taxa and populations, even in cases of limited genetic divergence.

Univariate analysis: significant osteoderm variation

The univariate analyses (ANOVA and ANCOVA) confirmed significant morphometric variation across osteoderm regions and sub-regions among species, particularly highlighting differences between genetically distinct taxa in the Acontinae (Daniels et al. 2005, 2009; Engelbrecht et al. 2013; Zhao et al. 2023). Consistent with previous research on lizard morphometrics (Revell 2009), our findings indicate that morphometric character measurement alone does not ideally explain the observed variation. Therefore, size-corrected variables are necessary to capture meaningful biological differences. The discovery of significantly higher variation in the C and D sub-regions aligns with previous research suggesting that certain morphological features retain higher phylogenetic

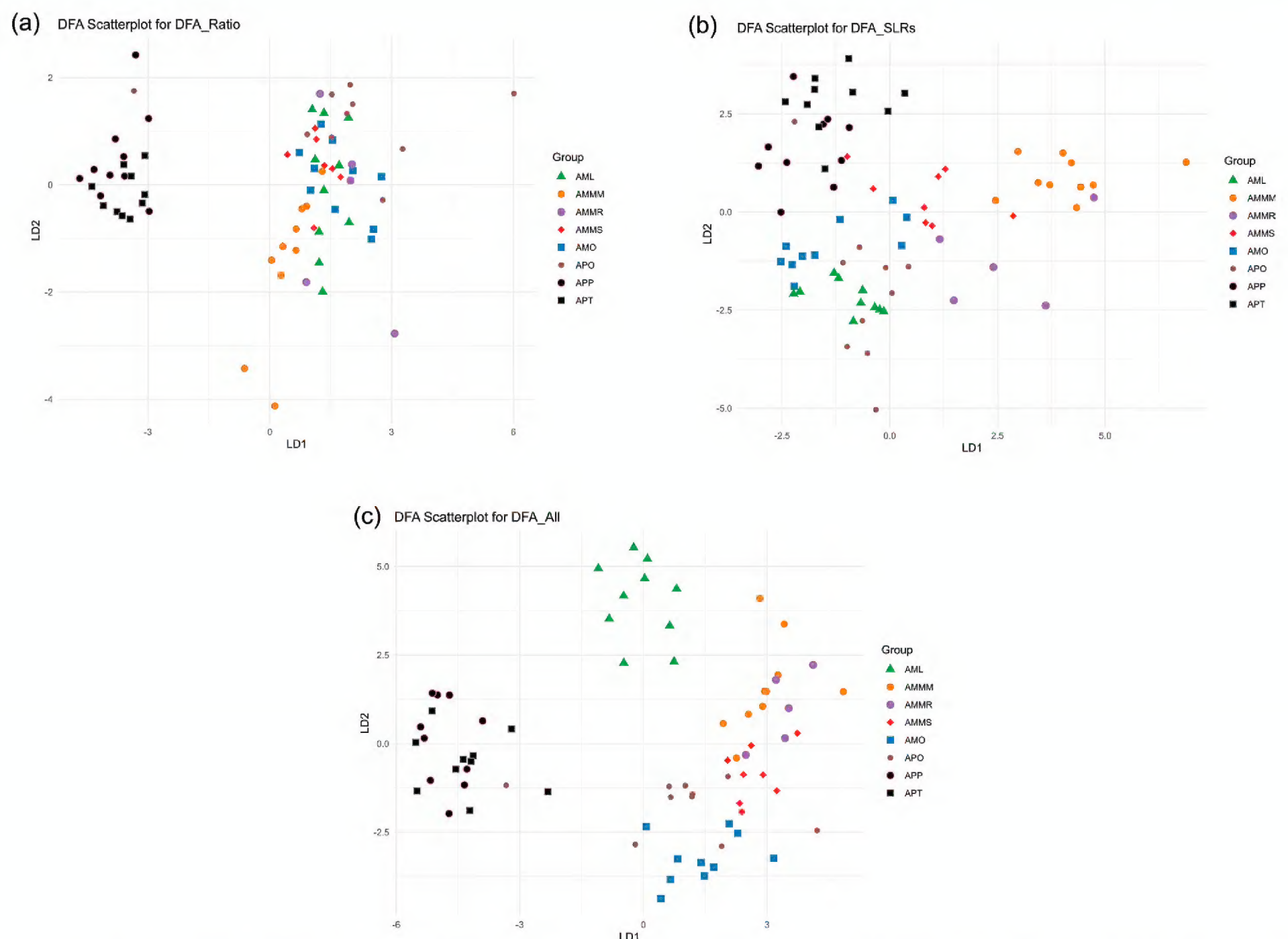


Figure 5. Discriminant function analysis (DFA) scatterplot of the first two discriminant functions, which capture the highest levels of total variance. The analysis was conducted independently using ratios, studentized linearized residuals (SLRs), and a combined approach. Abbreviations: “AMO” = *Acontias orientalis*, “AMMM” = *Acontias meleagris* (Mossel Bay population), “AML” = *Acontias lineicauda*, “AMMS” = *A. meleagris* (Saldanha Bay population), “AMMR” = *A. meleagris* (Robben Island population), “APO” = *Acontias occidentalis*, “APP” = *Acontias percivali*, and “APT” = *Acontias percivali tasmani*.

ic signals (Revell 2009). Interestingly, within the *A. meleagris* complex, the distinct morphometric characteristics of *A. p. tasmani* contradict previous genetic studies that suggest it is synonymous with *A. meleagris* (Daniels et al. 2005, 2009; Engelbrecht et al. 2013; Zhao et al. 2023). This result highlights the importance of osteoderm features, particularly in sub-regions C and D, for differentiating between morphs and populations where genetic divergence may be minimal or non-existent. Previous studies on morphological variation in reptiles support the notion that localized environmental pressures can drive phenotypic divergence, even in the absence of significant genetic differentiation (Losos et al. 1997; Arnold and Phillips 1999; Adams et al. 2004; Wiens et al. 2006).

Multivariate analysis: combining methods for enhanced discrimination

The principal component analysis (PCA) and discriminant function analysis (DFA) demonstrated the complementary strengths of using ratio-based and studentized linearized residuals (SLRs)-based metrics. Our results

showed that ratio-based PCA and DFA achieved better separation between genetic species, particularly *A. lineicauda*, *A. percivali*, and *A. occidentalis*, consistent with findings from genetic studies that identified these species as distinct evolutionary units (Daniels et al. 2005; Zhao et al. 2023). The relatively higher discrimination power for distinguishing genetic species in the ratio-based analysis underscores the utility of ratio-based metrics for assessing size-independent morphometric differences across broader taxonomic scales (Butler and King 2004).

However, within the *A. meleagris* group, the SLRs-based analysis was more effective at differentiating populations and morphs, suggesting that linearized residuals can capture subtle morphometric variations that ratios may miss. This observation aligns with studies that advocate for the use of multiple morphometric approaches to capture both coarse and fine-scale variation (Adams et al. 2004; Klingenberg 2016). The combined PCA and DFA analyses, which leveraged both ratio-based and SLRs-based data, yielded superior discrimination across all levels, reaffirming the importance of integrating multiple methods for robust morphometric analyses (Klingenberg 2016). Our DFA results also indicated that while morpho-

Table 1. Classification matrix from Discriminant Function Analysis with rows representing observed classifications and columns representing predicted classifications. The DFA was evaluated using F-tests with 12 and 54 degrees of freedom. The analysis was conducted independently using ratios (A), studentized linearized residuals (SLRs) (B), and a combined approach (C). Abbreviations: “AMO” = *Acontias orientalis*, “AMMM” = *Acontias meleagris* (Mossel Bay population), “AML” = *Acontias lineicauda*, “AMMS” = *A. meleagris* (Saldanha Bay population), “AMMR” = *A. meleagris* (Robben Island population), “APO” = *Acontias occidentalis*, “APP” = *Acontias percivali*, and “APT” = *Acontias percivali tasmani*.

Dataset		Correct percentage	AMO	AMMM	AML	AMMS	AMMR	APO	APP	APT
A.										
Ratio	AMO	70	7	1	1	0	0	1	0	0
	AMMM	80	1	8	0	0	1	0	0	0
	AML	80	0	1	8	1	0	0	0	0
	AMMS	25	2	0	2	2	0	2	0	0
	AMMR	20	1	1	0	1	1	1	0	0
	APO	80	1	0	0	0	0	8	1	0
	APP	80	0	0	0	0	0	0	8	2
	APT	100	0	0	0	0	0	0	0	10
	Total	71.2329	12	11	11	4	2	12	9	12
B.										
SLRs	AMO	60	6	0	1	1	0	2	0	0
	AMMM	100	0	10	0	0	0	0	0	0
	AML	90	0	0	9	0	0	1	0	0
	AMMS	75	1	0	0	6	0	0	1	0
	AMMR	60	0	1	0	1	3	0	0	0
	APO	70	0	0	2	0	0	7	1	0
	APP	90	0	0	0	0	0	0	9	1
	APT	80	0	0	0	0	0	0	2	8
	Total	79.4521	7	11	12	8	3	10	13	9
C.										
Combined	AMO	100	10	0	0	0	0	0	0	0
	AMMM	100	0	10	0	0	0	0	0	0
	AML	100	0	0	10	0	0	0	0	0
	AMMS	100	0	0	0	8	0	0	0	0
	AMMR	80	0	1	0	0	4	0	0	0
	APO	90	0	0	0	0	0	9	1	0
	APP	100	0	0	0	0	0	0	10	0
	APT	80	0	0	0	0	0	0	2	8
	Total	94.5205	10	11	10	8	4	9	13	8

metric variation across the broader anatomical osteoderm regions (MDB, MVB, MDT, and MVT) was significant, sub-regions C and D consistently provided greater discriminatory power. These sub-regions’ higher variance contribution suggests they may be more evolutionarily labile or subject to differential selective pressures (Vickaryous and Hall 2008; Stayton et al. 2018; Stayton 2024). The morphometric stability of sub-regions A and B across taxa suggests a possible conservation of osteoderm structure in these regions, potentially driven by functional constraints (Mouton et al. 2014; Stayton et al. 2018).

Taxonomic implications: osteoderm variation and species boundaries

Our findings offer new insights into the taxonomic boundaries within the *Acontias* genus. While molecular phylogenetics has been crucial for resolving species-level relationships, our morphometric analyses reveal that osteoderm characters provide valuable complementary data

for species delimitation. The distinct morphometric profile of *A. p. tasmani* suggests it may warrant re-evaluation as a separate evolutionary unit, despite its genetic similarity to *A. meleagris* (Daniels et al. 2005, 2009; Zhao et al. 2023). However, distinguishing between morphs and populations within the *A. meleagris* group highlights the limitations of osteoderm morphometrics in some cases, consistent with studies indicating that phenotypic plasticity can obscure genetic species boundaries, especially in taxa subject to rapid environmental change or adaptive radiation (Losos et al. 1997; Stayton 2024). These results underscore the need to integrate morphometric and genetic data for more accurate species delimitation. While genetic data are increasingly used for species identification, morphometric data can complement this by reflecting ecological and evolutionary processes not captured by genetic markers (Sites and Marshall 2004). Our combined approach enhanced discrimination between morphs and populations, suggesting that osteoderm morphometrics, when used alongside genetic data, can provide a more nuanced understanding of species boundaries (Sites

and Marshall 2003; Adams et al. 2004). Nevertheless, the significant controversy surrounding ratio-based size-correction methods highlights the errors and biases inherent in their use (Karp et al. 2012; Bartlett and Partnoy 2020). Furthermore, research has shown that ratio-based morphometric analyses do not fully eliminate the effects of size (Karp et al. 2012). It is therefore crucial to exercise caution when working with datasets that do not conform to isometric scaling.

Morphometric evolution and functional significance

The variation observed in osteoderm morphometrics across taxa and populations raises questions about the evolutionary and functional significance of these traits. Osteoderms, as dermal armor, play a crucial role in protection and structural support, and their morphological variation likely reflects adaptations to different ecological niches or selective pressures (Vickaryous and Sire 2009; Mahato 2018). The significant variation observed in sub-regions C and D, in particular, may reflect differential functional roles or responses to localized environmental conditions (Hanot et al. 2018; Mahato 2018). Interestingly, the lack of significant variation across the broader anatomical regions (MDB, MVB, MDT, MVT) suggests that osteoderm structure may be subject to stabilizing selection, with functionally critical regions exhibiting less morphological divergence (Vitt et al. 1997; Houssaye 2013). This hypothesis is supported by studies showing that certain osteoderm features are highly conserved across taxa, reflecting their importance in defensive behavior or other ecological functions (Mahato 2018; Inacio-Veenstra et al. 2022; Williams et al. 2022).

Limitations and future directions

While this study provides compelling evidence for the utility of osteoderm morphometrics in species delimitation and population differentiation, there are several limitations to consider. First, the ratio-based metrics are commonly used to assess size-independent morphological differences; they rely on the assumption of isometric scaling between traits and body size. This assumption may not always be valid, and deviations from isometry can lead to biases in the interpretation of morphological variation. Second, the reliance on two morphometric approaches (ratios and SLRs) may overlook other forms of variation, such as shape differences captured by geometric morphometrics (Zelditch et al. 2012). Future studies should explore the integration of geometric and traditional morphometric methods to provide a more comprehensive assessment of osteoderm variation. Third, while our combined approach significantly improved discriminatory power, the inability to consistently distinguish between morphs and populations within the *A. meleagris* group highlights the need for

additional data, such as environmental or behavioral traits, to fully resolve species boundaries (Wiens et al. 2006). The functional significance of the observed morphometric variation remains uncertain. Future research should investigate the ecological and evolutionary factors driving osteoderm evolution in *Acontias*, incorporating methods that account for allometric scaling to better assess size-independent morphological differences.

Conclusion

This study highlights the significant potential of osteoderm morphometrics for species delimitation and population differentiation within the legless lizard genus *Acontias*. Our findings underscore the importance of integrating multiple morphometric approaches to capture both broad-scale and fine-scale variation, particularly in taxa where genetic divergence may be minimal. By demonstrating the complementary strengths of ratio-based and SLRs-based methods, we provide a robust framework for future studies on reptilian morphometrics and evolutionary biology. Ultimately, our results contribute to a growing body of literature advocating for the use of morphometric data alongside genetic and ecological information to resolve taxonomic relationships in morphologically variable taxa. The findings have the potential to improve taxonomic resolution among skinks and contribute to broader taxonomic frameworks in herpetology.

Acknowledgement

We gratefully acknowledge the University of the Free State (UFS) for providing research facilities and funding through grant IFR2011041300046, which supported this project. We also extend our thanks to the South African Department of Environment and Nature Conservation (Permit No. FAUNA 624/2015) and the Department of Economic Development, Environment, and Tourism (Permit No. 001-CPM402-00001) for issuing the necessary collecting permits. We appreciate the ethical clearance provided by the UFS Ethical Committee (Animal Experiment No. NR04/2012 and NR07/2015), which was essential for the conduct of this research.

References

- Adams DC, Rohlf FJ, Slice DE (2004) Geometric morphometrics: ten years of progress following the 'revolution'. *Italian Journal of Zoology* 71: 5–16. <https://doi.org/10.1080/11250000409356545>
- Arnold SJ, Phillips PC (1999) Hierarchical comparison of genetic variance-covariance matrices. II. Coastal-inland divergence in the garter snake, *Thamnophis elegans*. *Evolution* 53: 1516–1527. <https://doi.org/10.1111/j.1558-5646.1999.tb05415.x>
- Bartlett RP, Partnoy F (2020) The Ratio Problem. SSRN. <https://doi.org/10.2139/ssrn.3605606>

- Baur H, Leuenberger C (2011) Analysis of ratios in multivariate morphometry. *Systematic Biology* 60: 813–825. <https://doi.org/10.1093/sysbio/syr061>
- Boulenger GA (1887) Catalogue of the Lizards in the British Museum (Natural History). British Museum (Natural History), London.
- Broeckhoven C, Diedericks G, Mouton PLFN (2015) What doesn't kill you might make you stronger: functional basis for variation in body armour. *Journal of Animal Ecology* 84:1213–1221. <https://doi.org/10.1111/1365-2656.12414>
- Branch WR (1998) Field guide to snakes and other reptiles of Southern Africa. Struik Publishers.
- Broadley DG, Greer AE (1969) A revision of the genus *Acontias* Cuvier (Sauria, Scincidae). *Arnoldia, Rhodesia* 4: 1–29.
- Burns ME (2008) Taxonomic utility of ankylosaur (Dinosauria, Ornithischia) osteoderms: *Glyptodontopelta mimus* Ford, 2000: a test case. *Journal of Vertebrate Paleontology* 28:1102–1109. <https://doi.org/10.1671/0272-4634-28.4.1102>
- Butler MA, King AA (2004) Phylogenetic comparative analysis: A modeling approach for adaptive evolution. *American Naturalist* 164: 683–695. <https://doi.org/10.1086/426002>
- Camp CL (1923) Classification of lizards. *Bulletin of the American Museum of Natural History* 48: 289–481.
- Courtenay LA (2023) Can we restore balance to geometric morphometrics? A theoretical evaluation of how sample imbalance conditions ordination and classification. *Evolutionary Biology* 50: 90–110. <https://doi.org/10.1007/s11692-022-09590-0>
- Daniels SR, Heideman NJ, Hendricks MG, Mokone ME, Crandall KA (2005) Unraveling evolutionary lineages in the limbless fossorial skink genus *Acontias* (Sauria, Scincidae): are subspecies equivalent systematic units? *Molecular Phylogenetics and Evolution* 34: 645–654. <https://doi.org/10.1016/j.ympev.2004.11.011>
- Daniels SR, Heideman NJ, Hendricks MG (2009) Examination of evolutionary relationships in the Cape fossorial skink species complex (*Acontinae*, *Acontias meleagris meleagris*) reveals the presence of five cryptic lineages. *Zoologica Scripta* 38: 449–463. <https://doi.org/10.1111/j.1463-6409.2009.00387.x>
- Daza JD, Stanley EL, Heinicke MP, Leah C, Doucet DS, Fenner KL, Bauer AM (2024) Compound osteoderms preserved in amber reveal the oldest known skink. *Scientific Reports* 14: 15662. <https://doi.org/10.1038/s41598-024-66451-w>
- Engelbrecht HM, Van Niekerk A, Heideman NJ, Daniels SR (2013) Tracking the impact of Pliocene/Pleistocene sea level and climatic oscillations on the cladogenesis of the Cape legless skink, *Acontias meleagris* species complex, in South Africa. *Journal of Biogeography* 40: 492–506. <https://doi.org/10.1111/jbi.12024>
- FitzSimons VFM (1943) The lizards of South Africa. *Transvaal Museum Memoirs* 1: 1–528.
- Fox J (2023) car: Companion to Applied Regression. R package version 3.1-1. <https://CRAN.R-project.org/package=car>
- Gross J, Ligges U (2015) nortest: Tests for normality. R package version 1.0-4. <https://CRAN.R-project.org/package=nortest>
- Hanot P, Herrel A, Guintard C, Cornette R (2018) The impact of artificial selection on morphological integration in the appendicular skeleton of domestic horses. *Journal of Anatomy* 232: 657–673. <https://doi.org/10.1111/joa.12772>
- Hewitt J (1929) On some Scincidae from South Africa, Madagascar, and Ceylon. *Annals of the Transvaal Museum* 13: 1–8. https://hdl.handle.net/10520/AJA00411752_685
- Hill RV (2005) Integration of morphological data sets for phylogenetic analysis of Amniota: The importance of integumentary characters and increased taxonomic sampling. *Systematic Biology* 54: 530–547. <https://doi.org/10.1080/10635150590950326>
- Hoffstetter R (1962) Observations sur les osteodermes et la classification des anguïdes et fossiles (Reptiles, Sauriens). *Bulletin of the Museum of the National History of Natal* 34: 149–157.
- Houssaye A (2013) Bone histology of aquatic reptiles: what does it tell us about secondary adaptation to an aquatic life? *Biological Journal of the Linnean Society* 108: 3–21. <https://doi.org/10.1111/j.1095-8312.2012.02002.x>
- Inacio-Veenstra LL, Broeckhoven C (2022) Revisiting the thermoregulation hypothesis of osteoderms: a study of the crocodilian *Paleosuchus palpebrosus* (Crocodylia, Alligatoridae). *Biological Journal of the Linnean Society* 135: 679–691. <https://doi.org/10.1093/biolinnean/blac001>
- Karp NA, Segonds-Pichon A, Gerdin AKB, Ramírez-Solis R, White JK (2012) The fallacy of ratio correction to address confounding factors. *Laboratory Animals* 46: 245–252. <https://doi.org/10.1258/la.2012.012003>
- Kassambara A (2016) Factoextra: extract and visualize the results of multivariate data analyses. R package version 1. <https://doi.org/10.32614/CRAN.package.factoextra>
- Klingenberg CP (2016) Size, shape, and form: Concepts of allometry in geometric morphometrics. *Development Genes and Evolution* 226: 113–137. <https://doi.org/10.1007/s00427-016-0539-2>
- Kuhn M (2015) caret: classification and regression training. *Astrophysics Source Code Library*, ascl-1505.
- Lamb T, Biswas S, Bauer A (2010) A phylogenetic reassessment of African fossorial skinks in the subfamily Acontinae (Squamata, Scincidae): Evidence for parallelism and polyphyly. *Zootaxa* 2657: 33–46. <https://doi.org/10.11646/zootaxa.2657.1.3>
- Lambiris AJL (1992) Preliminary remarks on the use of osteoderms as an adjunct to the taxonomy of Southern African lizards. *Journal of the Herpetological Association of Africa* 40: 14–18. <https://doi.org/10.1080/04416651.1992.9650310>
- Lê S, Josse J, Husson F (2008) FactoMineR: an R package for multivariate analysis. *Journal of Statistical Software* 25: 1–18. <https://doi.org/10.18637/jss.v025.i01>
- Lehmann R (2012) Improved critical values for extreme normalized and studentized residuals in Gauss–Markov models. *Journal of Geodesy* 86: 1137–1146. <https://doi.org/10.1007/s00190-012-0569-0>
- Lenth RV (2023) emmeans: Estimated Marginal Means, aka Least-Squares Means. R package version 1.8.9. <https://CRAN.R-project.org/package=emmeans>
- Losos JB, Warheitt KI, Schoener TW (1997) Adaptive differentiation following experimental island colonization in *Anolis* lizards. *Nature* 387: 70–73. <https://doi.org/10.1038/387070a0>
- Mahato NK (2018) Thoracolumbar transitional vertebrae: stages of osteological transition, mechanism of changes in zygapophyseal loading and orientation, and assimilation of mammillary processes. *Journal of Anatomy* 233: 394. <https://doi.org/10.1111/joa.12832>
- Mouton PLFN, Flemming AF, Broeckhoven C (2014) Generation gland morphology in cordylid lizards: an evolutionary perspective. *Journal of Morphology* 275: 456–464. <https://doi.org/10.1002/jmor.20227>
- Oliver JA (1951) Ontogenetic changes in osteodermal ornamentation in skinks. *Copeia* 1951: 127–130. <https://doi.org/10.2307/1437541>

- QGIS Development Team (2023) QGIS Geographic Information System. Open Source Geospatial Foundation Project. <https://qgis.org>
- R Core Team (2022) R: A language and environment for statistical computing (Version 4.2.2) [Software]. R Foundation for Statistical Computing. <https://www.R-project.org/>
- Revell LJ (2009) Size-correction and principal components for interspecific comparative studies. *Evolution* 63: 3258–3268. <https://doi.org/10.1111/j.1558-5646.2009.00804.x>
- Rohlf FJ (1990) Morphometrics. *Annual Review of Ecology and Systematics* 21: 299–316. <https://www.jstor.org/stable/2097027> <https://doi.org/10.1146/annurev.es.21.110190.001503>
- Signorell A, Aho K, Alfons A, Anderegg N, Aragon T, Arppe A, Borchers HW (2019) DescTools: Tools for descriptive statistics. R package version 0.99, 28: 17.
- Sites JW, Marshall JC (2003) Delimiting species: a Renaissance issue in systematic biology. *Trends in Ecology & Evolution* 18: 462–470. [https://doi.org/10.1016/S0169-5347\(03\)00184-8](https://doi.org/10.1016/S0169-5347(03)00184-8)
- Stayton CT (2024) Does Phenotypic Integration Promote Convergent Evolution? *Integrative and Comparative Biology* 64: 1484–1493. <https://doi.org/10.1093/icb/icae041>
- Stayton CT, O'Connor LF, Nisivoccia NM (2018) The influence of multiple functional demands on morphological diversification: a test on turtle shells. *Evolution* 72: 1933–1949. <https://doi.org/10.1111/evo.13561>
- Strahm MH, Schwartz A (1977) Osteoderms in the anguid lizard subfamily Diploglossinae and their taxonomic importance. *Biotropica* 9: 58–72. <https://doi.org/10.2307/2387862>
- Venables WN, Ripley BD (2002) MASS: Modern Applied Statistics with S. R package version 7.3-58. <https://CRAN.R-project.org/package=MASS>
- Vickaryous MK, Hall BK (2008) Development of the dermal skeleton in *Alligator mississippiensis* (Archosauria, Crocodylia) with comments on the homology of osteoderms. *Journal of Morphology* 269: 398–422. <https://doi.org/10.1002/jmor.10575>
- Vickaryous MK, Sire JY (2009) The integumentary skeleton of tetrapods: origin, evolution, and development. *Journal of Anatomy* 214: 441–464. <https://doi.org/10.1111/j.1469-7580.2008.01043.x>
- Vickaryous MK, Meldrum G, Russell AP (2015) Armored geckos: A histological investigation of osteoderm development in *Tarentola* (Phyllodactylidae) and *Gekko* (Gekkonidae) with comments on their regeneration and inferred function. *Journal of Morphology* 276: 1345–1357. <https://doi.org/10.1002/jmor.20422>
- Vitt LJ, Caldwell JP, Zani PA, Titus TA (1997) The role of habitat shift in the evolution of lizard morphology: evidence from tropical *Tropidurus*. *Proceedings of the National Academy of Sciences* 94: 3828–3832. <https://doi.org/10.1073/pnas.94.8.3828>
- Wiens JJ, Brandley MC, Reeder TW (2006) Why does a trait evolve multiple times within a clade? Repeated evolution of snakeline body form in squamate reptiles. *Evolution* 60: 123–141. <https://doi.org/10.1111/j.0014-3820.2006.tb01088.x>
- Williams C, Kirby A, Marghoub A, Kéver L, Ostashevskaya-Gohstand S, Bertazzo S, Vickaryous MK (2022) A review of the osteoderms of lizards (Reptilia, Squamata). *Biological Reviews* 97: 1–19. <https://doi.org/10.1111/brv.12788>
- Zelditch ML, Swiderski DL, Sheets HD, Fink WL (2012) Geometric morphometrics for biologists: A primer. 2nd edn. Academic Press.
- Zhao Z, Oosthuizen J, Heideman NJ (2021) How many species does the *Psammobates tentorius* (tent tortoise) species complex (Reptilia, Testudinidae) comprise? A taxonomic solution potentially applicable

to species complexes. *Journal of Zoological Systematics and Evolutionary Research* 59: 2189–2211. <https://doi.org/10.1111/jzs.12525>

- Zhao Z, Conradie W, Pietersen DW, Jordaan A, Nicolau G, Edwards S, Heideman NJ (2023) Diversification of the African legless skinks in the subfamily Acontinae (Family Scincidae). *Molecular Phylogenetics and Evolution* 182: 107747. <https://doi.org/10.1016/j.ympev.2023.107747>

Supplementary material 1

Supplementary information 1

Authors: Zhongning Zhao, Lucas Thibedi, Mphalile Mokone, Neil Heideman

Data type: xlsx

Copyright notice: This dataset is made available under the Open Database License (<http://opendatacommons.org/licenses/odbl/1.0/>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: <https://doi.org/10.3897/zse.101.138671.suppl1>

Supplementary material 2

Supplementary information 2

Authors: Zhongning Zhao, Lucas Thibedi, Mphalile Mokone, Neil Heideman

Data type: xlsx

Copyright notice: This dataset is made available under the Open Database License (<http://opendatacommons.org/licenses/odbl/1.0/>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: <https://doi.org/10.3897/zse.101.138671.suppl2>

Supplementary material 3

Supplementary information 3

Authors: Zhongning Zhao, Lucas Thibedi, Mphalile Mokone, Neil Heideman

Data type: xlsx

Copyright notice: This dataset is made available under the Open Database License (<http://opendatacommons.org/licenses/odbl/1.0/>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: <https://doi.org/10.3897/zse.101.138671.suppl3>

Supplementary material 4

Supplementary information 4

Authors: Zhongning Zhao, Lucas Thibedi, Mphalile Mokone, Neil Heideman

Data type: xlsx

Copyright notice: This dataset is made available under the Open Database License (<http://opendatacommons.org/licenses/odbl/1.0/>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: <https://doi.org/10.3897/zse.101.138671.suppl4>

Supplementary material 5

Supplementary information 5

Authors: Zhongning Zhao, Lucas Thibedi, Mphalile Mokone, Neil Heideman

Data type: xlsx

Copyright notice: This dataset is made available under the Open Database License (<http://opendatacommons.org/licenses/odbl/1.0/>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: <https://doi.org/10.3897/zse.101.138671.suppl5>

Supplementary material 6

Supplementary images

Authors: Zhongning Zhao, Lucas Thibedi, Mphalile Mokone, Neil Heideman

Data type: docx

Copyright notice: This dataset is made available under the Open Database License (<http://opendatacommons.org/licenses/odbl/1.0/>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: <https://doi.org/10.3897/zse.101.138671.suppl6>

Supplementary material 7

Supplementary information 7

Authors: Zhongning Zhao, Lucas Thibedi, Mphalile Mokone, Neil Heideman

Data type: xlsx

Copyright notice: This dataset is made available under the Open Database License (<http://opendatacommons.org/licenses/odbl/1.0/>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: <https://doi.org/10.3897/zse.101.138671.suppl7>

Supplementary material 8

Supplementary information 8

Authors: Zhongning Zhao, Lucas Thibedi, Mphalile Mokone, Neil Heideman

Data type: xlsx

Copyright notice: This dataset is made available under the Open Database License (<http://opendatacommons.org/licenses/odbl/1.0/>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: <https://doi.org/10.3897/zse.101.138671.suppl8>

Supplementary material 9

Supplementary information 9

Authors: Zhongning Zhao, Lucas Thibedi, Mphalile Mokone, Neil Heideman

Data type: xlsx

Copyright notice: This dataset is made available under the Open Database License (<http://opendatacommons.org/licenses/odbl/1.0/>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: <https://doi.org/10.3897/zse.101.138671.suppl9>